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Influence of disturbance on insect communities in Pacific Northwest streams

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Abstract

Coniferous forests of the Pacific Northwest provide a unique setting for stream ecology research because of the great age of the forests and the important role of wood debris in structuring aquatic systems. The composition and diversity of the insect community in Mack Creek, a stream in a 450 yr conifer forest, was compared with that in Grasshopper Creek where it flowed through a recent clearcut, and at Quartz Creek, which had a 40 yr deciduous canopy. Of the 256 taxa identified, Mack Creek had the highest species richness (196) and evenness. The open site had 191 taxa but high dominance of a few grazer taxa. The deciduous-canopy site had 165 taxa with abundant detritivores. Despite differences in density, the biomass of emergence was similar at the three sites, ranging from 1.53 to 1.65 g m^{-2} yr^{-1}.

The importance of disturbance in structuring stream communities was demonstrated in phenomenological studies after a debris torrent at Quartz Creek, and by monitoring stream recovery following the eruption of Mt. St. Helens in 1980. At Quartz Creek, the debris torrent eliminated the fauna from a 300 m reach, but there was rapid recovery. Emergence density in the same year was similar to that of the control site. The major shift in populations was a decrease in detritivores and moss associates and an increase in grazers, especially *Baetis* mayflies.

At Ape Creek on Mt. St. Helens, over 200 taxa were recorded by 1987 but most occurred in very low densities. This site is reset by winter freshets and by infilling with glacial fines in the summer so the fauna continues to be dominated by weedy, or early successional species. At Clearwater Creek, the presence of wood debris as a stable substrate and limited inputs of fine sediment after 1980 have hastened population recovery. A decade after the eruption this site can be characterized as being in the mid-stages of succession with high insect productivity from an algal-based food web. With further growth of the riparian vegetation I predict a shift towards a detritus-based food web and fauna more similar to Mack Creek than it is at present.

Introduction

Interdisciplinary ecological research in the Coniferous Forest biome received a major boost from the IBP funding in the early 1970's. The Stream Team at Oregon State University (OSU Stream Team) developed as a group of researchers studying factors affecting the structure and function of stream ecosystems. With biologists, hydrologists, geomorphologists, and foresters involved, there was a broad perspective on the watershed level, echoing the approach advocated by Hynes (1975) in his Baldi Lecture 'The Stream and Its Valley'. The aquatic entomological aspects of this research are the theme of this paper, but before addressing this topic it is necessary to put the project in the context of the unique Pacific Northwest landscape.

The Pacific Northwest region, dominated by coniferous forests, extends from northwestern California to the southwest coast of Alaska with the eastern boundary being the crest of the Coast Range or the Cascade Mountains. The region has wet mild winters and warm dry summers. Less than 10% of the precipitation falls during the summer and the evaporative demands are also much higher than in other temperate forests (Waring & Franklin, 1979).

These coniferous forests have the largest mass, both as living trees and as woody debris, of any forests in the world (Franklin *et al.*, 1981). Waring & Franklin (*op. cit.*) demonstrate that the structural characteristics – massiveness, evergreenness, large leaf areas, and needle-shaped leaves – are advantageous under the moisture, temperature, and nutrient regimes of the area. Mild winter temperatures permit winter photosynthesis, and cool summer nights make large leaf and other biomass components less costly to maintain than in other temperate forest regions. Also, conifers have lower nutrient requirements and use acquired nutrients more conservatively than do deciduous hardwoods. Since the large biomass accumulations are due to the sustained height growth and longevity (most of these species typically live >400 years), the absence of typhoons and hurricanes that frequent eastern Asia and eastern North America, is also a key element of conifer dominance in the Pacific Northwest (Waring & Franklin, *op. cit.*)

There are still some remnant stands of ancient forests in the Pacific Northwest, especially on public lands. However, even in the National Forests, clearcutting is proceeding at an alarming rate. The threat to the biotic diversity of this community is just as great as that in the tropical rainforests. In addition to terrestrial communities, the aquatic biota also may be at risk because the riparian zone exerts primary control over biotic associations in streams (Cummins *et al.*, 1984).

The conflict between demands for harvesting old growth for timber and those advocating its conservation as habitat for the northern spotted owl (*Strix occidentalis caurina* (Merriam)) has resulted in 'an embroglio of biological, economic, political, and social issues' (Strong, 1987). The owl is an indicator species for other components of the old-growth community, so management practices implemented on its behalf will be a major factor in determining the fate of an entire community and will demonstrate whether the nation intends to pay more than lip service to the principle of conserving biotic diversity (Simberloff, 1987).

The amount of large woody debris in these coniferous forests is equally as impressive as the huge accumulation of biomass. Much of the watershed and stream research has centered on the role of this debris in structuring the system and its importance as a nutrient sink (Triska *et al.*, 1982). Woody debris (> 10 cm dia) accumulates to 200 metric tons ha^{-1} on land. In small streams it may weigh 25–40 kg m^{-2} (Triska & Cromack, 1980).

Some conifer stands in the H. J. Andrews Experimental Forest of the Oregon Cascades are at least 450 years old, with Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and hemlock (*Tsuga heterophylla* (Raf.) Sarg.) trees that are 2 m diameter and 75 m tall. The Mack Creek drainage is included in a Long Term Ecological Research Site (LTER) and thus protected from logging. Mack Creek is considered a 'prototype' stream (*sensu* Cummins *et al.*, 1984) that has had minimal human impact since aboriginal times. Mack Creek is a valuable site as a reference point to learn how streams function in a pristine condition. Two examples from the literature recognize this need. Triska & Cromack (1980) have pointed out that aquatic insects evolved in systems where wood debris was far more abundant than it is today, but in almost all streams the wood has been removed before its role was understood. In discussing disturbance and the patch dynamics concept of stream ecology, Townsend (1989) stated: 'Information is needed about the benthic community before disturbance, about the spatial and temporal scale of events in the benthos, and about the sources of colonists....'. The data sets presented here address this list of requisites.

The two main objectives in this paper are: 1) to describe the composition and diversity, or species richness, of aquatic insect communities with particular reference to Mack Creek as a prototype stream; and 2) to elucidate the role of disturbance in structuring Pacific Northwest stream communities.

Insect communities in three riparian settings

Insect emergence was measured in 1982–83 as part of a comprehensive study of the impact of riparian vegetation on the structure and function of stream ecosystems. The purpose was to compare emergence as an index of secondary production in: a) Mack Creek, flowing through a 450 yr conifer forest; b) Grasshopper Creek in a recent clearcut; and c) Quartz Creek which was heavily shaded by a deciduous canopy of *Alnus* about 40 years after clearcutting.

All sites are on 3rd-order streams in the McKenzie River drainage on the western side of the Oregon Cascade Range (44°N, 122°W). In addition to the riparian treatment differences, the sites varied in elevation and gradient: Quartz Creek, 490 m, 5% gradient; Mack Creek, 800 m, 10% gradient; and Grasshopper Creek, 880 m, 9% gradient. I would have preferred sites more closely matched for altitude, but those available were dependent on the logging pattern; low altitude drainages were harvested in the 1940's, while steeper slopes at higher altitudes were logged more recently.

Four emergence traps (each 3.34 m^2) were used in each stream, two over riffles, and two over pools or drop zones. Large traps were needed to enclose the range of microhabitats that are found in cobble-boulder substrates. Further details of the sites and trapping procedures are given in Anderson *et al.* (1984).

Over 256 000 adults, representing >250 taxa in five orders, were collected from the three streams in one emergence season (Table 1). These are underestimates of both numbers emerging and of species richness because the traps were not operated from November to late March, and many Diptera, including Chironomidae, were identified only to genus. About 70 species of chironomids are listed for Mack Creek (Parsons *et al.*, 1991), but only 38 taxa are included in Table 1.

Temperature differences associated with altitude resulted in emergence being about a month earlier at Quartz Creek than at the other two sites. The early season emergence of stoneflies and chi-

Table 1. Number of taxa, density (no. m^{-2}), and dry biomass (mg m^{-2}) of aquatic insects in emergence traps in three Oregon Cascade Range streams, 1982–83.

	Mack Creek (450 yr conifer)			Quartz Creek (40 yr deciduous)			Grasshopper Creek (5 yr clearcut)			Combined
	No. of taxa	Density	Biomass	No. of taxa	Density	Biomass	No. of taxa	Density	Biomass	No. of taxa
Plecoptera	40	750	605	29	348	365	34	241	224	49
Ephemeroptera	35	358	377	31	446	415	38	739	726	43
Trichoptera	50	181	239	39	172	255	41	48	189	64
Megaloptera	2	<1	12	1	<1	5	1	<1	5	3
Diptera	69	4525	421	65	4133	485	77	2488	502	97
Chironomidae	(38)	(4389)	(284)	(38)	(4001)	(366)	(49)	(2372)	(401)	(53)
Tipulidae	(14)	(34)	(42)	(12)	(36)	(83)	(13)	(51)	(45)	(21)
Other Diptera	(17)	(102)	(95)	(15)	(95)	(37)	(15)	(65)	(56)	(23)
Total	196	5814	1654	165	5099	1525	191	3516	1646	256

ronomids that was missed would be greater at Quartz Creek than at Mack Creek or Grasshopper Creek. However, this does not account for the low numbers of taxa at this deciduous-canopy site; species richness is consistently lower in each of the major orders (Table 1) and the missing taxa are not spring emergers.

Of the total taxon pool, the old-growth site had the highest number of taxa (196), followed by the clearcut (191), and significantly fewer in the regrowth deciduous-canopy site (165). For Plecoptera, Trichoptera, and Ephemeroptera, where taxonomic resolution was at the species level (except for *Baetis*), the species richness ranking is: Mack, 125; Grasshopper, 113; and Quartz, 99. In summary, the majority of identified taxa were shared by all three sites. The prototype stream had the highest taxon richness (76% of those recorded) but it was followed closely by Grasshopper Creek (74%), the most recently disturbed site.

While density is important from the standpoint of biodiversity considerations, the biomass of populations is more relevant in comparing the functional role or trophic importance of the taxa. Despite differences in taxonomic composition at the three sites, total emergence is surprisingly similar (Table 1). The major difference is the low density of Chironomidae at Grasshopper Creek (2400 m^{-2} vs 4000). But the dominant chironomids at Grasshopper Creek were large Diamesinae so chironomid biomass was greater than at the other two sites and total biomass of emerging insects differed by less than 8% between the three sites.

The ranking of genera according to biomass reveals interesting patterns of dominance/diversity (Table 2). The old-growth site has the greatest evenness or the most balanced community with 10 genera accounting for 50% of emergence, compared with six at Quartz Creek and only four at Grasshopper Creek. As expected, the open site was dominated by algal grazers (e.g. *Baetis*, *Diamesa*, *Epeorus*, *Cinygmula*, *Allocosmoecus*), whereas the deciduous canopy site had more shredders and other detritivores (*Paraleptophlebia*, *Micropsectra*, *Polypedilum*, *Lepidostoma*, *Brillia*). Differences in community composition are thus at least partially explained by differences in the food resource base. However, irrespective of the riparian type, half of the taxa are common to the top 25 genera of all three streams.

Population recovery after a localized disturbance event

A rain-on-snow event in February 1986 caused severe flooding in mid-elevations of the Cascade Range and a debris torrent at Quartz Creek devastated the biota at the 1982–83 study site. The torrent originated as a landslide which sluiced a tributary to bedrock and travelled down Quartz Creek for 300 meters. It then set up a debris jam 40 m in length, 25 m in width and 5 m in height at a constriction in the channel. Where the study site previously had been densely shaded it was now open to full sunlight because the alder riparian strip was destroyed. Also, the cobble-boulder substrates were completely reworked and most of the woody debris and other organic materials were removed to the debris jam.

This event provided the opportunity to monitor the recovery of the benthic community in an area where a discrete stream reach had been reset to the earliest stages of succession. A detailed report of ecosystem recovery after this disturbance event is given by Lamberti *et al.* (1991). An upstream area was available for comparison where the riparian strip was intact and the stream channel was only slightly rearranged by the flood. The emergence study from 1982–83 (Tables 1 and 2) provided a unique data set for comparison with 1986. Emergence traps were deployed in the open devastated area and in the upstream control area from April through October, 1986.

The flood event had a detrimental effect on the benthic community upstream of the debris-torrent reach as all of the dominant genera (those accounting for 50% of the biomass, Table 2), had lower emergence in 1986 than in 1982–83. The number of insects emerging, excluding Chironomidae, in the upstream control was only 50% of that for 1982–83 (Table 3). The decrease was most apparent for many of the detritivores: Nem-

Table 2. Biomass of emerging insects from three Oregon Cascade Range streams in 1982–83. Data are expressed as mg m^{-2} yr^{-1} for the 25 most abundant genera at each site, and as cumultative percentage of total emergence.
D = Diptera; D–C = Diptera–Chironomidae; E = Ephemeroptera; P = Plecoptera; T = Trichoptera

	Mack Creek			Quartz Creek			Grashopper Creek		
		Weight	(%)		Weight	(%)		Weight	(%)
1	*Orthocladius* (D–C)	111.0	6.7	*Calineuria* (P)	204.1	13.4	*Baetis* (E)	385.0	23.4
2	*Moselia* (P)	94.8	12.4	*Paraleptophlebia* (E)	158.8	23.8	*Diamesa* (D–C)	186.1	34.7
3	*Cinygmula* (E)	94.7	18.2	*Micropsectra* (D–C)	119.6	31.6	*Orthocladius* (D–C)	131.1	42.7
4	*Baetis* (E)	90.5	23.6	*Baetis* (E)	100.4	38.2	*Epeorus* (E)	107.2	49.2
5	*Agathon* (D)	83.9	28.7	*Polypedilum* (D–C)	92.9	44.3	*Cinygmula* (E)	74.9	53.7
6	*Lepidostoma* (T)	79.2	33.5	*Alloperla* (P)	86.1	49.9	*Allocosmoecus* (T)	62.6	57.7
7	Despaxia (P)	78.9	38.3	*Lepidostoma* (T)	72.6	54.7	*Ameletus* (E)	61.1	61.2
8	*Alloperla* (P)	65.5	42.2	*Brillia* (D–C)	64.0	58.9	*Taenionema* (P)	39.5	63.6
9	*Epeorus* (E)	62.5	46.0	*Rhyacophila* (T)	45.5	61.9	*Rhyacophila* (T)	38.2	66.0
10	*Calineuria* (P)	54.2	49.3	*Cinygmula* (E)	43.7	64.7	*Paraleptophlebia* (E)	34.9	68.1
11	*Zapada* (P)	53.6	52.5	*Orthocladius* (D–C)	37.3	67.2	*Agathon* (D)	34.4	70.2
12	*Paraleptophlebia* (E)	46.9	55.4	*Tipula* (D)	36.1	69.5	*Calineuria* (P)	33.5	72.2
13	*Rhyacophila* (T)	44.0	58.0	*Glossosoma* (T)	31.5	71.6	*Alloperla* (P)	31.8	74.1
14	*Yoraperla* (P)	40.5	60.5	*Epeorus* (E)	28.3	73.5	*R. verrula* (T)	29.2	75.9
15	*Pteronarcys* (P)	39.9	62.9	*Neophylax* (T)	25.9	75.2	*Yoraperla* (P)	26.6	77.5
16	*Conchapelopia* (D–C)	39.2	65.3	*Holorusia* (D)	22.5	76.6	*Rhithrogena* (E)	18.4	78.6
17	*Paraleuctra* (P)	36.3	67.4	*Agathon* (D)	22.1	78.1	*Pedicia* (D)	17.7	79.7
18	*Parametriocnemus* (D–C)	31.6	69.4	*Rhithrogena* (E)	21.7	79.5	*Parametriocnemus* (D–C)	16.9	80.7
19	*Micropsectra* (D–C)	28.7	71.1	*Parametriocnemus* (D–C)	20.9	80.9	*Zapada* (P)	15.8	81.7
20	*Ironodes* (E)	27.8	72.8	*Ameletus* (E)	19.8	82.2	*Zavrelimyia* (D–C)	15.8	82.7
21	*Sweltsa* (P)	27.0	74.4	*Ironodes* (E)	18.8	83.4	*Neophylax* (T)	13.8	83.5
22	*Soyedina* (P)	26.2	76.0	*Despaxia* (P)	18.4	84.6	*Conchapelopia* (D–C)	12.8	84.3
23	*Dolophilodes* (T)	21.4	77.3	*Malenka* (P)	18.1	85.8	*Sweltsa* (P)	12.8	85.1
24	*Heleniella* (D–C)	18.5	78.4	*Dolophilodes* (T)	16.7	86.9	*Serratella* (E)	11.5	85.8
25	*Ameletus* (E)	18.1	79.5	*R. verrula* (T)	12.9	87.7	*Ironodes* (E)	11.4	86.5
Total emergence (g m^{-2} yr^{-1})		1.65			1.53			1.65	

ouridae, *Alloperla*, *Paraleptophlebia*, *Lepidostoma*, *Polypedilum*, and *Brillia*.

With the apparent reduction in numbers of insects in the control reach in 1986, it was remarkable to note the resiliency of the community in the open debris-torrent reach (Table 3). Most of the common stream insects were able to exploit this new habitat within a few months, a pattern described by Townsend & Hildrew (1976) in their study of drift and recolonization of denuded substrates as the 'continuous redistribution of the benthos'. The dominant taxon was *Baetis* which had 4–5 times more emergence in the impacted area than in either the control or the earlier study (Table 3). *Baetis* is a browser-scraper of periphyton. It is multivoltine and abundant in the drift so its ability to exploit a new habitat is to be expected.

Data on the Trichoptera community at Quartz Creek in 1986 were analyzed in detail for comparison with emergence trap results for 1982–83 (Anderson *et al.*, 1984). The number of species recorded in the debris-torrent area (39) was similar to that for 1982–83 (38) (Table 4). About 10 species from 1982–83 were absent in 1986, but this was balanced by the appearance of a similar number of previously unrecorded species. With a few exceptions (*Rhyacophila verrula* Milne, *Lepidostoma cascadense* (Milne), *Heteroplectron californicum* McLachlan, and Hydroptilidae), the presence/absence changes of Trichoptera were in species with <5 specimens in the 1982–83 col-

Table 3. Changes in density of emerging adults after a flood and debris torrent in February, 1986, affected the study site at Quartz Creek, Lane Co., OR.

	1982–83	1986	
		Upstream (shaded) control	Impacted (open) area
	(No. m^{-2} yr^{-1})	(No. m^{-2} yr^{-1})	(No. m^{-2} yr^{-1})
Plecoptera	348.4	98.8	116.2
Ephemeroptera	445.7	310.5	930.8
(Baetis)	(158.0)	(131.4)	(635.9)
(Paraleptophlebia)	(197.2)	(71.3)	(148.2)
Trichoptera	172.4	146.1	80.9
Diptera	4132.5	3593.4	3412.1
(Chironomidae)	(4001.4)	(3480.4)	(3332.8)
(Tipulidae)	(36.0)	(34.7)	(16.6)
(Other Diptera)	(95.1)	(78.3)	(62.7)
Total density	5099.0	4148.8	4540.0

lections. The Plecoptera species list also was similar before (28) and after (29) the debris torrent, with three additional species in 1986 and two from 1982–83 not found in 1986 (R. W. Wisseman, pers. com.).

Two families in the Rhyacophiloidea had a positive response to the new habitat (Table 4). The Glossosomatidae are scrapers and were 3–4 times more abundant from July onward in the open area compared with the closed-canopy site. *Glossosoma* has two generations per year, which explains the population increase in the summer. The hydroptilids are also multivoltine. The summer generation probably developed from eggs deposited in the open area, rather than from downstream drift of larvae.

All the taxa of herbivore-shredders and piercers listed in Anderson *et al.* (*op. cit.*) were affected by this disturbance. *Micrasema bactro* Ross, the one species of Brachycentridae previously recorded, was the fourth most abundant caddisfly in 1982 but, after the flood, its density decreased by a factor of four in both the shaded control and impacted reach (Table 4). As *M. bactro* is moss-associated, the habitat disruption by the flood had the same impact as did the debris torrent. The same reasoning is invoked to explain the fate of *Rhyacophila verrula*. This is an atypical species of *Rhyacophila* in that it is a moss and algae feeder rather than a predator. In 1982 it was the third most common *Rhyacophila* but in 1986 no specimens emerged in either the control or impacted sections. In contrast, the Hydroptilidae, or microcaddisflies, had a positive response following perturbation. In the open reach there were three genera that were previously unrecorded and the numbers emerging were 5–10 times greater than in either 1982 or in the upstream shaded area (Table 4).

It is reemphasized that not only have most species been able to colonize the new habitat created by the debris torrent but the individuals also had completed development to the adult stage during the same summer. Multivoltine taxa, such as Chironomidae, Simuliidae, *Baetis* and *Glossosoma* are amongst the successful colonizers but most of the species emerging in the impacted area had a univoltine life cycle.

Recolonization responses after the Mt. St. Helens eruption

In contrast to the debris torrent at Quartz Creek, which was a severe but localized disturbance, the eruption of Mt. St. Helens (46° 12′N, 122° 11′W) on May 18, 1980, devastated more than 390 km^2. The biota in several major drainages

Table 4. Changes in taxonomic composition and density of emerging Trichoptera adults after a flood and debris torrent in February, 1986, affected the study site at Quartz Creek, Lane Co., OR.

	1982–83		1986			
			Upstream (shaded) control		Impacted (open area)	
	No. of species	Density (No. m^{-2})	No. of species	Density (No. m^{-2})	No. of species	Density (No. m^{-2})
Rhyacophiloidea						
Rhyacophilidae	15	18.6	16	25.6	14	6.1
Glossosomatidae	3	32.2	2	19.8	2	41.2
(Apr.–June)		(24.0)		(10.0)		(6.4)
(July–Oct.)		(8.2)		(9.8)		(34.8)
Hydroptilidae	1	0.4	1	0.9	4	5.5
Hydropsychoidea						
Philopotamidae	4	28.6	5	39.2	4	11.5
Psychomyiidae	1	5.9	1	33.7	1	0.5
Polycentropodidae	1	3.4	2	8.1	2	3.1
Hydropsychidae	3	2.9	2	3.6	3	2.8
Limnephiloidea						
Limnephilidae[1]	5	5.8	5	1.8	2	1.1
Lepidostomatidae	3	57.8	3	9.2	2	5.3
Brachycentridae	1	16.5	1	3.9	2	3.8
Calamoceratidae	1	0.3	1	0.3	0	–
Total species	38		39		38	
Total density		172.4		146.1		80.9

[1] Includes Uenoidae.

was nearly eliminated and the physical structure of stream channels was greatly altered. Sites at Ape Canyon and Clearwater Creek that were affected by the eruption have been studied to monitor the benthic community recovery after the eruption.

Ape Canyon – Qualitative monitoring of recolonization

Ape Creek is a 2nd-order stream, 5–6 km long, flowing ENE from Mt. St. Helens through a steep gorge and canyon to its junction with Smith Creek and thence to the Muddy River. It originates in Ape Glacier at 1500 m and drops precipitously to 800 m in the first 3 km. The study area, <8 km from the crater, is in the lower canyon where the stream is relatively low gradient and the valley floor is 200–300 m wide. Several small streams and seeps enter the creek from both sides of the canyon (Fig. 1). These tributaries, which were important in the recolonization process, are not glacially fed.

According to Janda *et al.* (1981), the mud flow, or lahar, that devastated Ape Canyon was 10–20 m deep. It swept down the canyon at 30–40 m sec^{-1} destroying the riparian forest and scouring the canyon to bedrock through much of its length. Later eruptions blanketed the side slopes and canyon floor with tephra, ranging in size from ash particles to fist-sized chunks of pumice.

The pronounced instability of the substrates has been a major factor affecting recovery of the

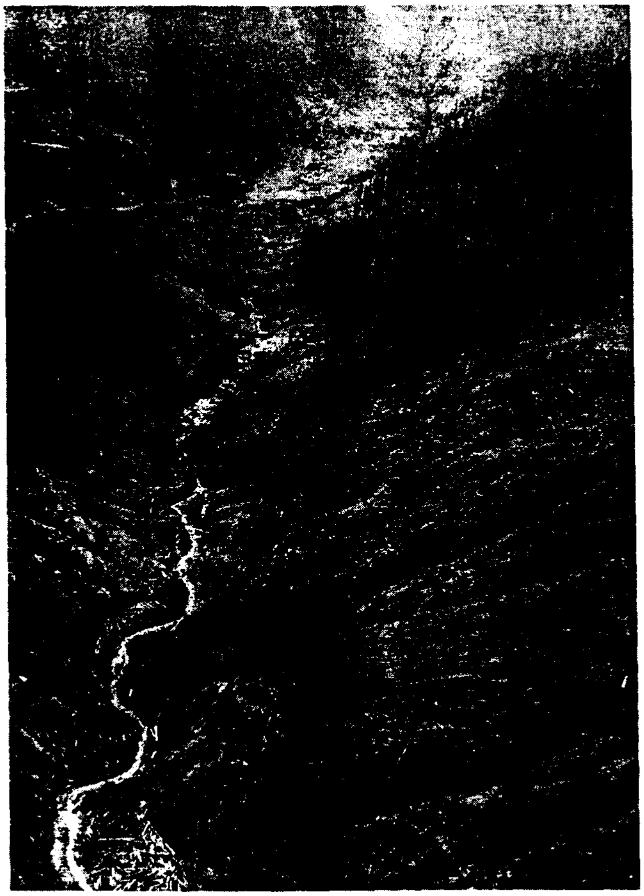

Fig. 1. Aerial view looking upstream, of Ape Canyon, Mt. St. Helens, Skamania Co., WA, taken in 1985. Depth of the mudflow that scoured the canyon on May 18, 1980, is evident especially where trees border the site. Note the prevalence of side-wall tributaries and amount of wood debris on the canyon floor.

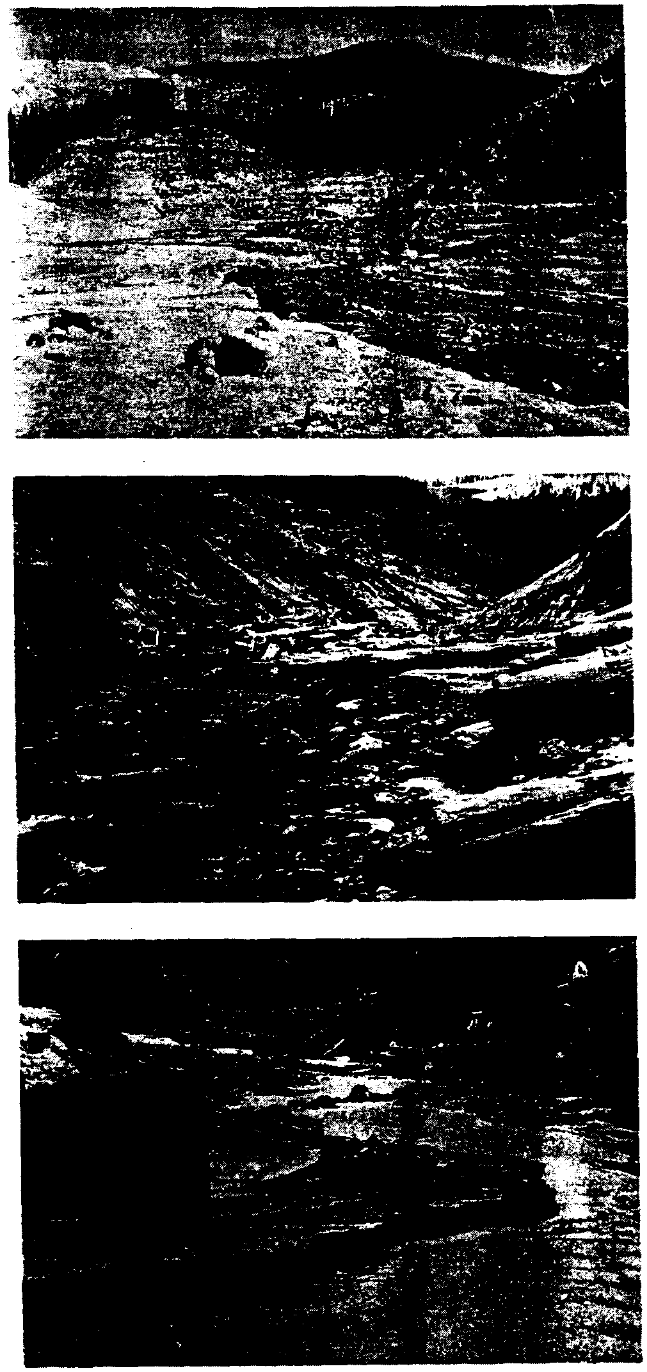

Fig. 2. Ape Creek, Skamania Co., WA, as a variable habitat after the eruption of Mt. St. Helens: 2a September 1980, a broad shallow stream with a shifting bed of fine sand: 2b January 1981, after winter freshets had flushed out the fine sediments: 2c September 1981, after glacial melt water refilled the channel with fine sediments.

stream biota. In September 1980, Ape Creek was broad and very shallow (width:depth ratio 128:1) with a shifting bed of fine sand (Fig. 2a). The water was extremely turbid with both ash and pumice in transport. Freshets in the winter of 1980–81 changed the appearance of the canyon and resorted the stream bed (Fig. 2b). Large logs from the hillslopes littered the canyon floor and fine sediments were flushed out, leaving a stream bed of cobble and boulders. In January 1981, the water was crystal clear and the incised channel had a W:D ratio of 47:1.

Stable substrates and improved water quality provided ideal conditions for recolonization in 1981. Light levels were high because of clear water and the absence of a canopy, so diatoms and green algae built up rapidly. Early colonists, primarily Chironomidae, attained densities of 24000 m^{-2} by July 1981. However, the habitat reverted to 1980 conditions when the bed was filled with glacial fines after Ape Glacier began to melt in late summer. The W:D ratio increased to 164:1 and the stream biota crashed as a result of both scouring and smothering by fine sediment (Fig. 2c).

The sequence of winter flushing followed by in-filling with fine sediment after the glacier began to melt in hot weather also occurred in succeeding years. The pattern and magnitude of these disturbances depended on the weather conditions of a given year. There is a 'window' for biological activity in spring and early summer, and (usually) a crash by August or September due to deposition of glacial fines. Taxa with early-season emergence and short life cycles are favored in this habitat. At this site it is not just a case of arriving there, but of surviving in an unstable, and short-season, habitat.

Ape Creek was impoverished even after the first winter freshet; only 15 insects were collected in 10 samples (each 0.05 m^2) from September 1980 and January 1981. However, qualitative collections from canyon-wall seeps and small tributaries in September 1980 contained 34 taxa: 27 Chironomidae, 3 Rhyacophilidae, 2 Baetidae, 1 Tipulidae, and 1 Simuliidae. In four visits to the site from May to October 1981 the taxon list of early colonizers was increased to 98. Of these, 79 were from the creek and 19 were collected only in the tributaries or seeps (Table 5). The cumulative number of taxa recorded from Ape Canyon had a lower annual rate of increase after 1981 but the continued addition of new records demonstrated that, even though 200 taxa had been recorded by 1987, the site was not fully colonized.

The cumulative list indicates that the taxa have occurred at the site but gives no indication of their persistence. For example, the only dragonfly larva collected was found in 1980. A somewhat better index is species richness. Combining the data to include both early and late-season collections in each interval illustrates the general increase in species richness for Ape Canyon since the eruption: 1980–81, 98 taxa; 1982–85, 129 taxa; 1986–87, 141 taxa.

Most species occurred in very low densities and, over the entire period, 71 taxa were collected only once. In 1980 and 1981, 22 taxa (16 chironomids) were recorded that were not found in later years. Records for these unsuccessful colonists may reflect the intensity of collecting effort as the chance of finding rare species was enhanced by extensive qualitative collections. This was es-

Table 5. Colonization pattern of invertebrates at Ape Canyon, Mt. St. Helens, WA., for 7 years following the May 18, 1980, eruption. Data are expressed as the cumulative number of taxa recorded from Ape Creek. The total taxa including those collected from tributaries and seeps is given in brackets.

	1980		1981		1982		1983		1984		1985		1986		1987	
Ephemeroptera	2	(3)	3	(4)	5	(6)	6	(6)	8	(8)	8	(10)	14	(17)	16	(18)
Plecoptera	0	(0)	3	(3)	6	(6)	6	(7)	9	(11)	9	(11)	11	(12)	12	(13)
Odonata	1	(1)	1	(1)	1	(1)	1	(1)	1	(1)	1	(1)	1	(1)	1	(1)
Rhyacophilidae	0	(3)	1	(4)	1	(5)	3	(6)	7	(10)	7	(10)	8	(11)	8	(12)
Other Trichoptera	0	(0)	3	(3)	5	(6)	6	(7)	9	(9)	9	(10)	10	(12)	15	(17)
Coleoptera	1	(1)	3	(3)	5	(5)	5	(6)	7	(8)	7	(8)	8	(9)	9	(10)
Chironomidae	2	(27)	48	(62)	56	(70)	56	(71)	57	(71)	60	(74)	67	(79)	73	(86)
Simuliidae	0	(1)	2	(2)	7	(9)	7	(9)	7	(9)	7	(9)	7	(9)	9	(11)
Tipulidae	1	(1)	4	(4)	6	(6)	6	(6)	6	(6)	6	(7)	6	(7)	10	(14)
Other Diptera	1	(1)	7	(7)	9	(9)	10	(12)	11	(13)	11	(13)	12	(14)	13	(16)
Non-insects[1]	0	(0)	4	(5)	5	(5)	6	(6)	6	(6)	6	(6)	6	(6)	6	(6)
Total – Creek	8		79		106		112		128		131		150		172	
Total – Canyon		38		98		128		137		152		159		177		204

[1] Identified only to higher categories: Oligochaeta, Nematoda, Turbellaria, Acarina, Copepoda, Ostracoda.

pecially the case for chironomids; several thousand exuviae were collected from foam collections in September, 1980, and May and July, 1981, and identified by Dr. W. P. Coffman.

Chironomidae were overwhelmingly dominant in the recovery sequence. They accounted for 42% of the taxa at Ape Canyon and 80–90% of the numbers and biomass of all invertebrates collected in eight years. Their ability to exploit new habitats is apparent in that they accounted for 63% of the taxa recorded through 1981, whereas by 1987 they were only 42% of the total taxa (Table 5).

The tributaries and seeps are important in recolonization of Ape Canyon because they are potential refugia for avoiding the deleterious effects of infilling by glacial fines in the summer as well as being the original 'seed' source of some colonists after the 1980 eruption. Excluding the 71 taxa collected only once from either the creek or the tributaries (which cannot be shared), the overlap between habitats was 85%. Thus, although mainstem Ape Creek is a distinctly different habitat from that in the smaller tributaries, the contribution of the latter to recolonization and survival in Ape Canyon cannot be ignored.

Though rapid recolonization occurred at Ape Canyon, the fauna was still dominated by early successional species in 1987. As a stream in an old-growth Cascade Range forest, Mack Creek (Tables 1 and 2) would be expected to have a fauna similar to that in the Mt. St. Helens area prior to the eruption. Collections in Ape Canyon were mostly of larvae that were identified to genus. Species-level determinations would add to the Ape Creek list (Table 5) but this cannot account for the missing 60+ species of mayflies, stoneflies, and caddisflies that are found at Mack Creek.

Clearwater creek – Quantitative monitoring for ten years of recolonization

This study site is about 15 km, NE of Mt. St. Helens, at an altitude of 750 m near the Upper Clearwater Bridge. The trees in the Clearwater Valley were levelled by the lateral blast during the eruption. The stream channel received a heavy impact from blast deposits; about 30–70 cm of ash and pumice were deposited, in addition to massive amounts of wood debris with some logs 2 m diameter. Clearwater Creek is a 3rd-order stream with a discharge ranging from 0.2 to $> 10\ m^3\ sec^{-1}$ It flows through a broad valley and is relatively low gradient. Substrates in the immediate area are largely sand and gravel, whereas further upstream, where the gradient increases, there is a larger proportion of cobble and much of the mobile material was flushed out in the first 1–2 years after the eruption. The site is described more fully by Anderson & Wisseman (1987).

The Clearwater Valley is more accessible than is Ape Canyon because the road system has been maintained even after salvage logging of the blown down timber. The area was replanted with Douglas-fir within 2–3 years after the eruption and the riparian area was planted with deciduous species (*Salix* and *Populus*) by 1984. Biologists began monitoring Clearwater Creek within 2–3 months after the eruption. Quantitative benthos samples were taken for 10 years, at least in late summer of most years. In 1980–83 the samples were collected by OSU Stream Team biologists. The data for 1985–89 are from the intensive study by Meyerhoff (1991).

In late summer of 1980, the stream beds of both Ape Creek and Upper Clearwater Creek were primarily shifting sand and pumice, but wood debris also was available as a stable habitat in the latter. Twice as many taxa were collected from wood as in benthos samples (23 vs 11, with Chironomidae = 1 taxon) at Clearwater Creek (Dudley & Anderson, 1982). The fauna were typical benthic taxa without a significant component of xylophilous species so the wood basically served as a refuge and as a substrate for the aufwuchs layer. A collection of pupal exuviae in September, 1980, contained at least 32 species of Chironomidae (W. P. Coffman, pers. com.). It is likely that most of these were using wood debris, rather than shifting mineral substrates, for their larval habitat.

In addition to the species that survived on site, recolonization was effected by drift from tributaries and by aerial dispersal. As at Ape Creek the successful early colonists were Diptera, especially Chironomidae. Based on a study of caddisfly dispersal, Anderson & Wisseman (*op. cit.*) concluded that establishment or survival of larvae was limiting rather than the failure of adults to arrive at the site. Up to 1985, caddis larvae were uncommon although about 40 species had been collected. By contrast, 69 species of adult Trichoptera were collected at a light trap from July to September 1985 (Anderson & Wisseman *op. cit.*). Seven species of adult dytiscid beetles, mostly *Oreodytes* spp, have been recorded but few larvae were collected.

Species richness in annual benthos samples has increased throughout the first decade after the eruption, although at a slower rate for the last 5 years (Fig. 3). Taxonomic composition changed significantly in that, while the number of chironomid taxa increased up to 1983, their dominance as a proportion of the total species pool decreased from 75% in 1980 to 30% in 1989. The number of EPT taxa (Ephemeroptera, Plecoptera, Trichoptera) has progressed steadily from 3 in 1980 to 50 in 1989. EPT diversity ($H' \log_2$) increased from < 1.0 to > 3.0, whereas chironomid midge diversity only varied from 3.2 to 3.6 (Meyerhoff, 1991).

Population density in the late-summer samples from Clearwater Creek was relatively stable at 15–20 000 m^{-2} from 1982 to 1985, with the standing crop being about 1 g m^{-2} (Fig. 4). After 1985 there was a jump to a new level of 50–75 000 m^{-2} or 3–5 g m^{-2}. This increase is attributed to: a) arrival of additional colonizing species; b) further stabilization of substrates; and c) an increase in the range of available food sources.

A decade after the Mt. St. Helens eruption, the Clearwater Creek site can be characterized as being in the mid-stages of succession, with high productivity due to absence of a closed canopy and the resulting high light levels. With further

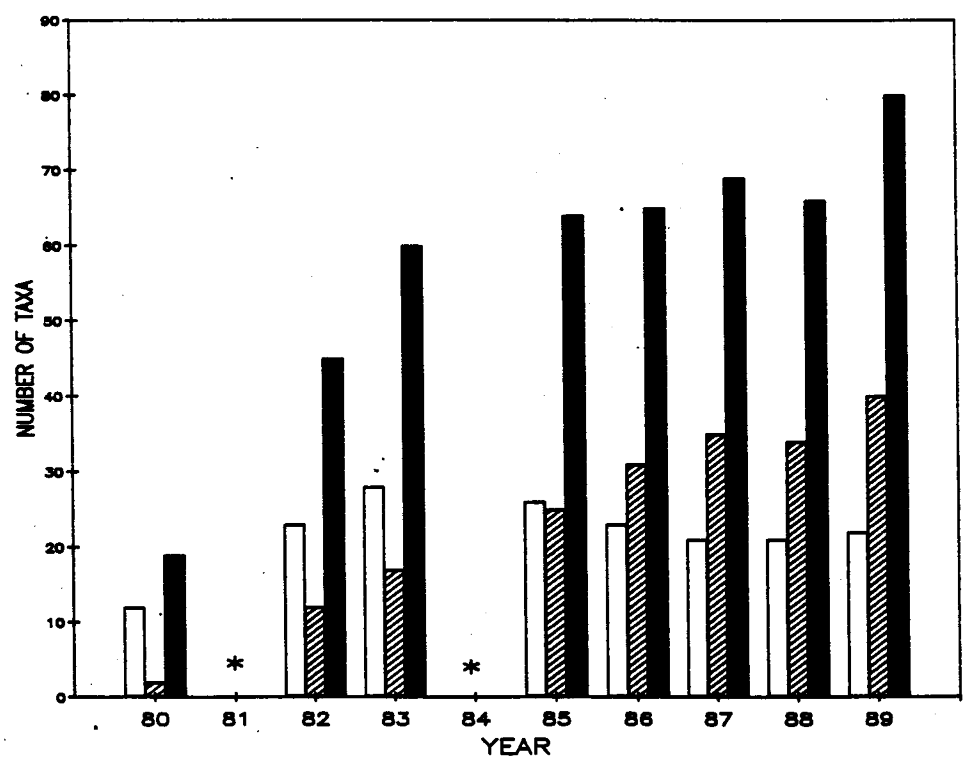

Fig. 3. Number of taxa from Clearwater Creek, Skamania Co., WA, collected in late-summer quantitative samples for 10 years after the eruption of Mt. St. Helens. Open bars-Chironomidae; hatched bars-EPT taxa (Ephemeroptera, Plecoptera, & Trichoptera); solid bars-all taxa. Quantitative samples were not taken at the appropriate times in 1981 and 1984.

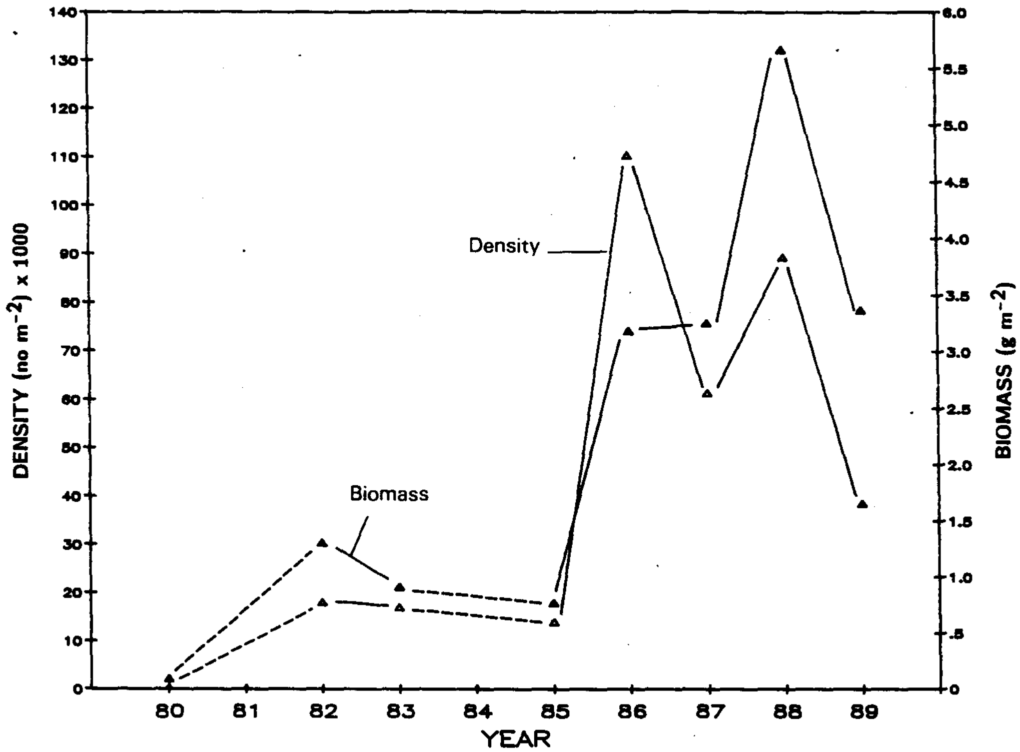

Fig. 4. Density (open symbols) and biomass (closed symbols) of insects in late-summer benthos samples from Clearwater Creek, Skamania Co., WA, for 10 years following the eruption of Mt. St. Helens.

growth of the riparian vegetation, I predict a shift towards a detritus-based food chain and a more 'balanced' fauna. This would involve a decrease in density of Diptera and Ephemeroptera and some increases in the proportion of caddisflies, stoneflies, and elmid beetles.

Discussion

The two approaches used in these projects were: (1) comparative studies of streams with contrasting disturbance regimes; and (2) phenomenological accounts of particular events. Townsend (1989) discussed the relative merits and shortcomings of these compared with experimental approaches, and argued that many more phenomenological studies of disturbance and its influence are required. The continued monitoring of Quartz Creek since the 1986 debris flow as part of the LTER program (Lamberti *et al.*, 1991) is a significant contribution in disturbance ecology. The importance of the temporal axis as recognized by both Ward (1989) and Townsend (*op. cit.*), is very much a feature of our studies of stream insect communities.

Community composition is strongly influenced by disturbance and colonization within a patchy environment. Townsend (*op. cit.*) states that the highly disturbed nature of streams does not necessarily mean that their community composition will be more variable than that of less disturbed systems. Kerst & Anderson (1975) noted that it was somewhat anomalous to refer to a 'stable community in an unstable habitat' but that this seemed to be the case with a Plecoptera community of >40 species in a small Oregon stream. Species composition and diversity had not changed appreciably in 40 years despite the fact that the stream bed was commonly scoured and redeposited to a depth of 20–30 cm by winter storms, and major floods had a return frequency of 20 years. They attributed the high diversity to 'pulse stability' – regular but acute physical disturbances that maintained the system at an intermediate phase of development. Most species occur in low numbers and very few species are favored for a long enough period to establish dominance to the extent that their congeners are excluded.

The overall study comparing Cascade Mountain streams with different types of riparian vegetation had as a major tenet that streamside vegetation exerts primary control over biotic associations (Cummins *et al.*, 1984). The emergence-trap data for aquatic insects supports this concept in that Mack Creek, the prototype stream, had the greatest species richness and evenness of Ephemeroptera, Plecoptera, and Trichoptera. The strong dominance due to grazers at Grasshopper Creek is obviously related to the lack of canopy at that site. While the perturbation was due to clearcutting, even in pristine streams a similar effect could result from beaver activity, wildfire, or debris torrents. Compared with Grasshopper Creek, the deciduous-canopied site at Quartz Creek indicated a shift to more detritivores that utilized the inputs of allochthonous leaf litter. All sites had similar levels of standing crop biomass. Taken together, data for the three streams demonstrate that differences in riparian vegetation have added both food-base and habitat heterogeneity with a concomitant increase in species richness for the drainage basin.

The taxon list for these cool mountain streams of the Pacific Northwest (Table 1) contrasts sharply with that of Big Sulphur Creek in northern California, studied by McElravy *et al.*, (1989). They emphasize washout from winter storms as a major determinant of community composition. However, in seven years they only recorded 81 taxa, or about one-third of the number that occur in the Oregon sites. The impoverished nature of Big Sulphur Creek may also be related to thermal stress (August max = 23.6 °C) and chemical composition of the water.

The phenomenological accounts of stream disturbance demonstrate the inter-relationships of the spatial and temporal scales in the recovery sequence. The debris torrent at Quartz Creek denuded ca. 300 m of stream bed and the adjacent riparian strip but it was recolonized by a major component of the typical benthic community within a few months. This level of disturbance appears to increase biodiversity by opening up habitat patches and adding to the complexity of the physical habitat as well as to the variety of autochthonous and allochthonous foods.

By any standards, the eruption of Mt. St. Helens was a megadisturbance event for stream communities in several watersheds. The remarkable resiliency of the stream fauna is apparent in that 100 taxa had been collected in Ape Canyon by 1981 and 200 by 1987. Most of these would fit in the category 'variously referred to as weedy, fugitive, ruderal or *r*-selected' (Townsend, 1989). Relatively few were able to build up to high densities under the frequently disturbed conditions of this site.

The 10-year monitoring of benthos at Clearwater Creek indicates a progressive improvement in the habitat and a two-step sequence in community recovery. The 4–5 fold increase in density and standing crop after 1985 is attributed to stabilization of the stream bed, along with the arrival of additional colonizing species and some increase in the variety of food resources associated with growth of riparian trees. The change in community composition, with increases in EPT taxa and a decrease in chironomid taxa, may reflect a gradual change towards the type of community found in Mack Creek. However, it will require monitoring beyond the year 2000 before the trajectory of the postdisturbance recovery sequence becomes clear.

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